A unifying framework for the transient parasite dynamics of migratory hosts

Stephanie J. Peacock*, Martin Krkošek, Mark A. Lewis, Péter K. Molnár

Supplemental information

Model equations

We applied the model developed by Peacock et al. (1), consisting of seven partial differential equations. Here, we give the equations as applied in this study, ignoring processes such as host birth, natural host mortality, and within-host reproduction of parasites that were included in the original model. These simplifying assumptions were made in order to focus on the parasite-related impacts on the host population specific to environmentally transmitted macroparasites during migration. As described in the main text, we considered three versions of the model: (1) a base model that describes migratory escape, (2) a model including parasite-induced migratory culling, and (3) a model including stationary hosts and parasite induced stopping of hosts (Table S1). In all three versions, the change in the density of free-living parasite larvae at point x, $L(x,t)$, in the environment is given by:

$$\frac{\partial L}{\partial t} = \lambda\left(PH + \hat{P}\hat{H}\right) - \mu_L L - \beta L\left(H + \hat{H}\right) \quad \text{(S1)}$$

where λ is the rate at which adult parasites produce larvae, $P(x,t)$ and $\hat{P}(x,t)$ are the mean parasite burdens of stationary and moving hosts, respectively, $H(x,t)$ and $\hat{H}(x,t)$ are the densities of stationary and moving hosts, respectively, μ_L is the natural mortality rate of larvae, and β is the rate at which larvae are ingested (or otherwise taken up) per host.

The equations describing changes in the density of migrating hosts, $\hat{H}(x,t)$, their mean parasite burden, $\hat{P}(x,t)$, and the variance-to-mean ratio, $\hat{A}(x,t)$, depended on the version of the model under consideration (Table S1).

* Corresponding author: stephanie.peacock@ucalgary.ca

Table S1. Equations for the three cases of the migratory host – macroparasite model that we applied. See Fig. 1 for graphical description and Table 1 for description of parameters and assumed values in simulations.

	Base model (escape)	Culling	Stalling
Host population density	$\frac{\partial \hat{H}}{\partial t} - c\frac{\partial \hat{H}}{\partial x} = 0$	$\frac{\partial \hat{H}}{\partial t} - c\frac{\partial \hat{H}}{\partial x} = -\alpha \hat{P}\hat{H}$	$\frac{\partial \hat{H}}{\partial t} - c\frac{\partial \hat{H}}{\partial x} - \theta \hat{P}\hat{H}$ $\frac{\partial H}{\partial t} = \theta \hat{P}\hat{H}$
Mean parasite burden	$\frac{\partial \hat{P}}{\partial t} - c\frac{\partial \hat{P}}{\partial x} = \beta L - \mu_P \hat{P}$	$\frac{\partial \hat{P}}{\partial t} - c\frac{\partial \hat{P}}{\partial x} = \beta L - \mu_P \hat{P} - \alpha \hat{A}\hat{P}$	$\frac{\partial \hat{P}}{\partial t} - c\frac{\partial \hat{P}}{\partial x} = \beta L - \mu_P \hat{P} - \theta \hat{A}\hat{P}$ $\frac{\partial P}{\partial t} = \beta L - \mu_P P + \frac{\theta \hat{P}\hat{H}}{H}\left(\hat{A} + \hat{P} - P\right)$
Variance-to-mean ratio	$\frac{\partial \hat{A}}{\partial t} - c\frac{\partial \hat{A}}{\partial x} = \left(1 - \hat{A}\right)\left(\frac{\beta L}{\hat{P}} + \mu_P\right)$	$\frac{\partial \hat{A}}{\partial t} - c\frac{\partial \hat{A}}{\partial x} = \left(1 - \hat{A}\right)\left(\frac{\beta L}{\hat{P}} + \mu_P + \alpha \hat{A}\right)$	$\frac{\partial \hat{A}}{\partial t} - c\frac{\partial \hat{A}}{\partial x} = \left(1 - \hat{A}\right)\left(\frac{\beta L}{\hat{P}} + \mu_P + \theta \hat{A}\right)$ $\frac{\partial A}{\partial t} = (1 - A)\left(\frac{\beta L}{P} + \mu_P\right)$ $+ \frac{\theta \hat{H}\hat{P}}{HP}\Big(\hat{A}\big(3\hat{P} + 2\hat{A} - 1 - A$ $- 2P\big) + \left(\hat{P} - P\right)^2 - A\hat{P}\Big)$

Long-term equilibrium

In the base model, we consider the extreme case where the migration speed, c, approaches zero. In this case, we expect that the possibility of migratory escape is at its minimum (as hosts are not moving), and that the corresponding equilibrium parasite burden therefore represents an upper limit for the burdens that we would expect to see when hosts migrate at $c > 0$. Setting $c = 0$, we solved for the equilibrium parasite burden, $\hat{P}^*(x,t)$:

$$0 = \beta L^* - \mu_P \hat{P}^*, \tag{S2a}$$

$$\hat{P}^* = \frac{\beta L^*}{\mu_P}. \tag{S2b}$$

Inserting eq. (S2b) into the equilibrium equation for $L^*(x,t)$ yields:

$$0 = \lambda\left(\frac{\beta L^*}{\mu_P}\right)\hat{H}^* - \mu_L L^* - \beta L^* H^*. \tag{S3}$$

Eqs (S2b) and (S3) have a single solution at $L^*(x,t) = 0, \hat{P}^*(x,t) = 0$. This implies that eventually, parasite burdens will decline to zero regardless of the parameter choices, even in the limiting case where *c* = 0. Given that we anticipate parasite burdens will be less when *c* > 0 (i.e., migration reduces parasite burdens), we can assume that $L^*(x,t) = 0, \hat{P}^*(x,t) = 0$ for c > 0. Adler and Kretzschmar (2), who developed the non-spatial version of this model with stationary hosts only, found that a positive solution for $\hat{P}^*(x,t)$ (or $x^*(t)$ in their notation) exists when host birth exceeds host death. In our simulations we have assumed that both host birth and natural host death are zero in order to focus on the dynamics during migration, and so the result that $L^*(x,t) = 0, \hat{P}^*(x,t) = 0$ is consistent with the finding of Adler and Kretzschmar (2).

Initial conditions for simulations

We assumed migrating hosts had a spatial Gaussian distribution initially centered at *x* = 0 km with a standard deviation of 30 km (Fig. S1b). The total migrating host population summed to 10,000 individuals. For simulations of migratory stalling that included a stationary host population, we had to include a non-zero number of stationary hosts ($H(x,t_0) = 0.1$) to start because $H(x,t)$ appears in the denominator of terms in the equations for stationary parasite burden and variance-to-mean ratio (Table S1). The parasite burden and variance-to-mean ratios were constant at $\hat{P}(x,t_0) = P(x,t_0) = 5$

per host and $\hat{A}(x, t_0) = A(x, t_0) = 7.25$, corresponding to an overdispersion parameter in the negative binomial distribution of $k = \frac{P(x,t_0)}{A(x,t_0)-1} = 0.8$.

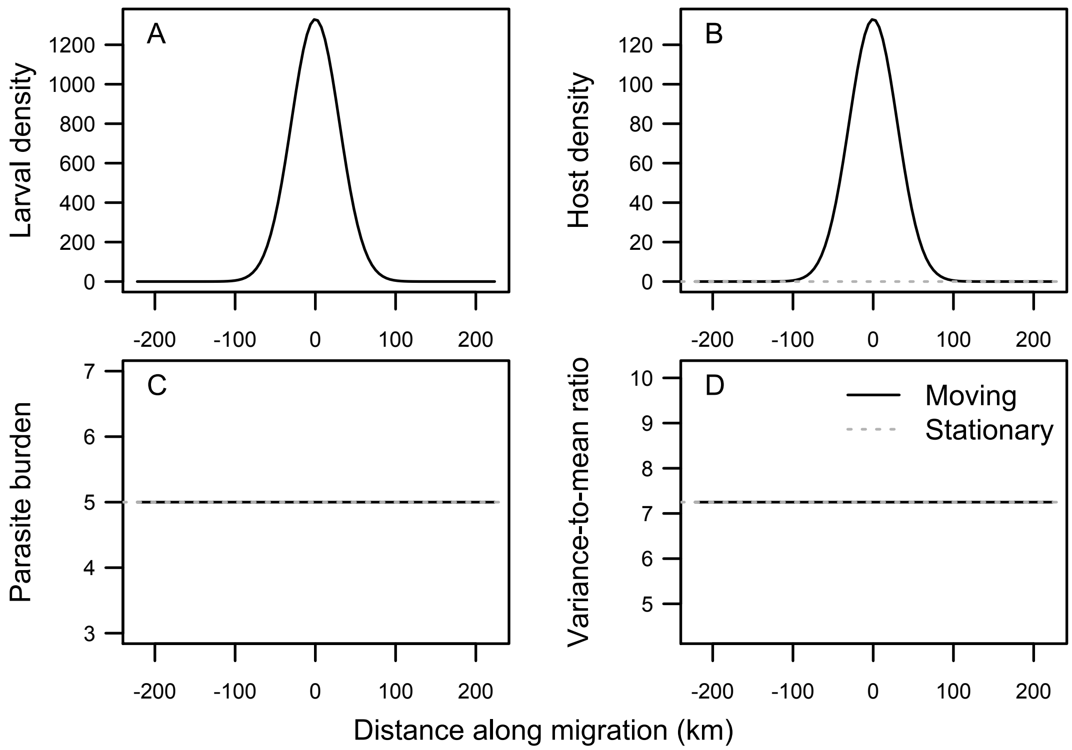

Fig. S1. Initial conditions for the model described in Fig. 1 and by equations (S1) and Table S1. A) The density of free-living larvae, $L(x,t = 0)$. B) The densities of stationary (H(x,t = 0)) and moving ($\hat{H}(x, t = 0)$) hosts. C) The mean parasite burdens of stationary (P(*x, t* = 0)) and moving ($\hat{P}(x, t = 0)$) hosts. D) The variance-to-mean ratios for the parasite burden among stationary (A(*x, t* = 0)) and moving ($\hat{A}(x, t = 0)$) hosts.

Supplemental results

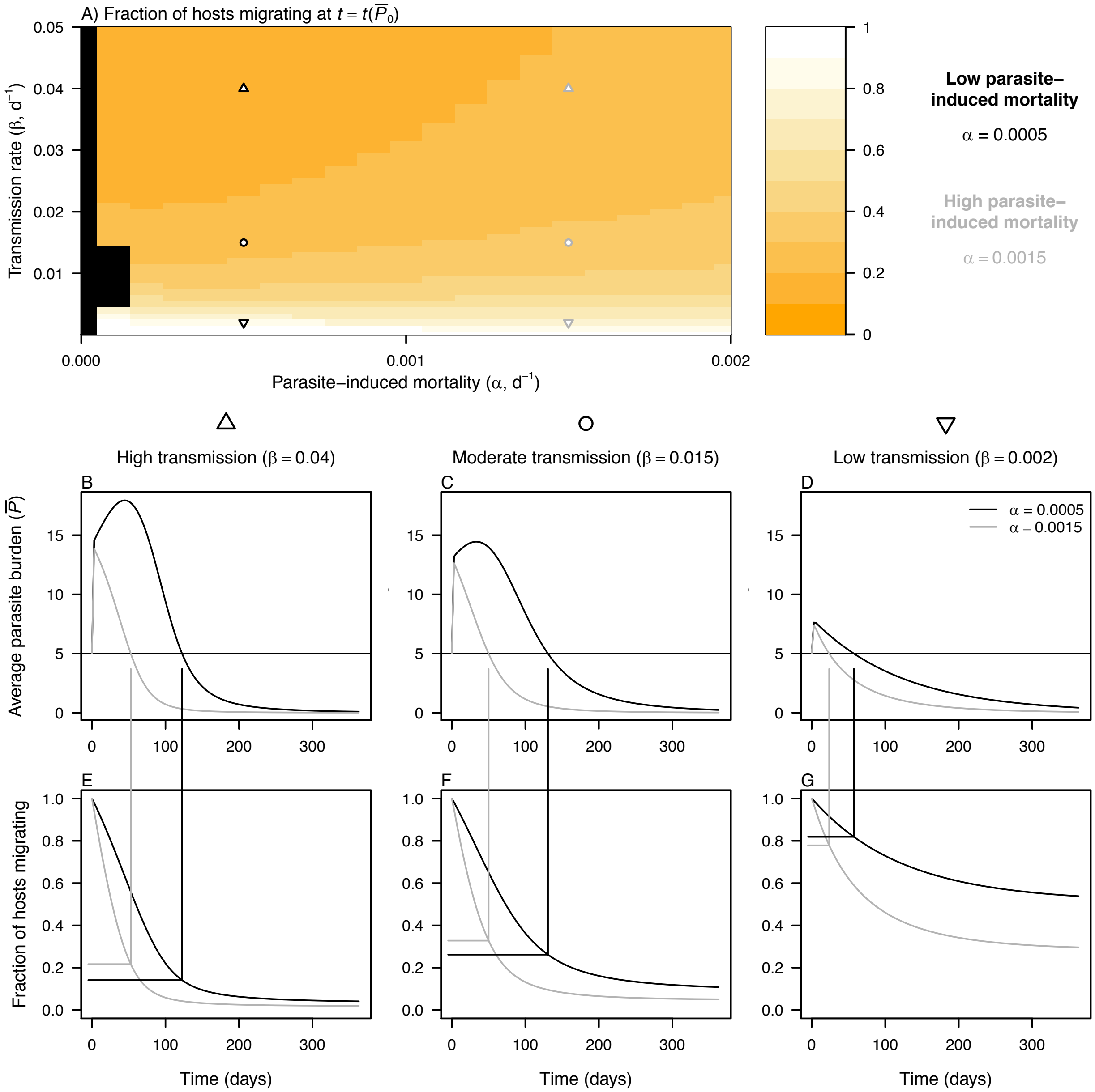

Fig. S2. A) The fraction of hosts migrating (i.e., the proportion alive given that $\theta = 0$) when parasite burdens decline to initial values ($\hat{P}(x, t_0) = P(x, t_0) = 5$ per host) over a range of parasite-induced mortality (x-axis) and transmission rates (y-axis) (see also Fig. 4D). Dynamics over the course of the migration for parameter combinations indicated by black and grey points are shown in (B-G): (B-D) The mean parasite burden of migrating hosts over the course of the migration for low (black) and high (grey) parasite-induced mortality. (E-G) The fraction of hosts migrating when parasite burdens decline to initial, with line segments illustrating the proportions at the time when parasite burdens decline to initial, shown in A. The proportion of hosts alive is consistently higher at the same point in time when parasite-induced mortality is low. However, because it takes longer for parasite burdens to decline to initial under low parasite-induced mortality, the proportion of hosts alive at that time is actually lower under high parasite-induced mortality and moderate to high transmission rates (E-F). At low transmission rates (D,G), peak parasite burdens are much lower and migratory culling is weaker, so the time to initial is less affected by parasite-induced mortality (Fig. 4B) and the proportion of hosts alive at time to initial decreases with increasing parasite-induced mortality as one might expect.

Literature cited

1. Peacock SJ, Bouhours J, Lewis MA, Molnár PK (2018) Macroparasite dynamics of migratory host populations. *Theor Popul Biol* 120:29–41.
2. Adler FR, Kretzschmar M (1992) Aggregation and stability in parasite-host models. *Parasitology* 104:199–205.